HAWAII IBP SYNTHESIS:
8. ISLAND ECOSYSTEMS: WHAT IS UNIQUE ABOUT THEIR ECOLOGY?

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We may now ask the question whether we have found anything unique or different in the ecology of island ecosystems from our studies. This is not an easy question.

It is clear that the biological evolution of our island ecosystems has been rather unique. Four factors stand out which contribute to the unique biological evolution of ecosystems here. These are the extreme isolation of the island group, the small size of the island habitats, the recency of the oceanic islands as a group, and their perturbation history in connection with volcanism.

The extreme isolation had a significant "screening effect" on what organism groups could get here and establish themselves successfully. This screening effect excluded any plants with large seeds or small seeds of short longevity. It also excluded among animals, all terrestrial mammals (except the hoary bat), large reptiles, and primates, except man.

The small size of the island habitats is the result of small island land masses jutting high out of the ocean. Thus, we have distinct altitudinal segregations of habitats with their own temperature regimes. Furthermore, these small land masses are segregated into windward (pluvio tropical) and leeward (xerotropical) habitats with their own rainfall regimes. The habitats are further fractioned by great variations in substrate, ranging from recent volcanic flows to old, sceletized, and nutrient-depauperated latosols. This island habitat mosaic brings about another factor of important ecological consequences, and that is the very limited recurrence of similar habitats across the island chain. These narrow habitat dimensions strongly limit the population sizes of the island biota.

The recency of oceanic islands as a group is undoubtedly of evolutionary significance also. They originated in the Tertiary, when the modern angiosperm flora had already evolved. In contrast, some of the continental tropical ecosystems evolved without major geological disturbances forming a primary succession from seed fern forests to primitive gymnosperm and angiosperm forests to modern angiosperm forests. These continental ecosystems developed during a much greater evolutionary time span.

The high tree species diversity of some continental tropical forests may be largely attributable to this.

Volcanism causes major geological disturbances. These perturbations are a significant part of island ecosystem development from the highest mountain top to sea level. Volcanic perturbations are of many kinds and differing degrees and are erratic or unpredictable. They were once effective on each island and left their traces long after individual volcanoes became extinct. As such they had and still have a great effect on the evolution of the island biota.

There is little doubt then, that the island biota evolved under unique environmental conditions. Much has been written also about their adaptive characteristics, which sometimes resulted in the development of rather bizarre island life forms. But has this also made the ecology of island ecosystems different?

The answer, as revealed from our studies, appears to be that ecological principles do not differ for island ecosystems. However, our studies have brought out some new dimensions to island ecosystem ecology, which should add to both their scientific understanding and appropriate management.

Distributional Characteristics of Island Biota

The spatial distribution analysis along the Mauna Loa mountain gradient confirmed Whittaker's individualistic species distribution model established for temperate mountains. It also confirmed the spatial association model of species distribution which is, in part, an affirmative answer to MacArthur's question on species and community patterns in the tropics. However, spatially associated species groups along environmental gradients are not to be considered unique for tropical areas, since such patterns have been demonstrated many times also in temperate environments. They are, like Whittaker's individualistic species distribution patterns, a universal phenomenon applicable to islands and continents, temperate and tropical environments alike.

However, we found a number of other distribution trends, all of them more or less wide-ranging (e.g., bimobal, multi-modal, and broadly overlapping). These all reflect generalistic tendencies of species behavior. The high proportion of these generalists in our biota groups are perhaps characteristic for geologically young areas or those relatively poor in species. This tendency may not be found in geologically older areas, and thus also not so much on older volcanic islands.

An island characteristic, which may have interesting applications, is that soil fungi, soil algae, and soil arthropods are probably mostly indigenous. This would imply as a hypothesis that they may form a community-similarity link with continental

mountain habitats in similar climatic and soil regimes. Conversely, the other island community members, the higher plants, birds, canopy arthropods, tree borers, and Diptera flies all form much more unique species compositions.

Community Structure and Niche Differentiation

Island communities have the same gross-structural characteristics as found in continental communities. For example, montane tropical rain forests and lava tube ecosystems are also found on continents. At the species level, our island communities are almost totally unique. But they are not so unique at the higher taxon level. At this higher level one can find interesting similarities and departures from continental ecosystems.

In our community structure analysis we focussed on the general niche level, a functional ecological unit concept, intermediate between the individual species and the total ecosystem. We identified general niches by species of closely similar function and structure, i.e., by life-form types (i.e., synusiae in plants, guilds in animals).

We did not really find "empty niches" in the sense of absence of important life forms among the native species. The life-form spectra appeared complete in all organism groups analyzed, i.e., plants, birds, canopy arthropods, and cave animals. This does not mean that "empty niches" may not be found in other island ecosystems, but it may imply that the empty niche phenomenon is probably an exception rather than a rule in developed island ecosystems. What appeared to be a departure from continental ecosystems of similar kind was that several important life-form groups had only one or a few native species, often with high quantitative importance. These appeared to occupy the more stable positions (or general niches) in the ecosystems in the sense that few exotics had invaded them. Conversely, exotic species invasion appeared to occur more readily in those general niches or life-form groups in which several native species occur with relatively small populations. However, this is a new hypothesis, which needs further testing. We have not yet given special attention to the ecology and relative stability of rare and endangered native species, which as a rule are probably more specialized.

Instead our studies brought out the ecological versatility of some of the dominant native island biota. For example, in the Kilauea rain forest, all native tree species can grow on mineral soil and as epiphytes. The same applies to most of the herbaceous native ferns. This phenomenon argues for the stability of native species composition under temporarily adverse forest floor conditions (e.g., pig disturbance, flooding, ash blanket deposits).

It is probable that ecological generalists among the native species prevail in the island ecosystems, which we analyzed. Both the Kilauea rain forest and the lava tubes are relatively young ecosystems, which support biota which are able to survive perturbation effects associated with volcanism. Frank Howarth mentioned the underground dispersal modes for the Hawaiian cave fauna. Thus, here we are dealing largely with biota, which are still displaying pioneering traits, a charactistic which all island biota must have had for becoming successfully established in the new island environment.